STUDIES IN ARACEAE

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(WITH PLATES IV–VI)

I. Nephthytis Gravenreuthii

In the fall of 1906 the writer enjoyed the privilege of examining the extensive collection of tropical aroids in the greenhouses of the New York Botanical Gardens, and of collecting material for an investigation of the embryo sac and embryo. Among other species, *Nephthytis Gravenreuthii* was selected for this purpose. A considerable amount of material was obtained, illustrating stages from the archesporium to the mature embryo.

Ovary.—The genus is characterized by a single simple carpel which shows a tendency toward a slightly unsymmetrical development, the stylar canal never being in the axis of the carpel (*fig. 2*). The carpel is short and thick, the stylar canal very short, funnel-shaped, and lined with viscid conducting cells. On the interior of the carpel the conducting cells reach a considerable length and come in contact with the ovule on all sides, sometimes reaching quite to the micropyle.

Ovule.—The ovary contains a single, basal, anatropous, cauline ovule. Probably the single, basal, orthotropous ovule is the most primitive kind, and in Arisaema we find an orthotropous ovule, but there are typically four ovules; and while they are cauline in origin they occur as lateral outgrowths of a suppressed placenta, the ill-defined point of the placenta representing the axis of the flower. The single axial ovule, even though it be anatropous, is no doubt a simpler type than this; and when we compare it with such a form as Dieffenbachia, in which each ovule, arising from the partially suppressed placenta, is surrounded by a separate carpel, its primitive character becomes yet more apparent.

In general, the ovule of the species now under discussion is peculiar for its massive integuments and for the poor development of the nucellus. The latter consists at first of a single row of cells surrounded by an epidermal layer (*fig. 1*). The hypodermal archesporial cell usually gives rise to two sporogenous cells; and one case of three sporogenous cells was discovered. In every case when observation was possible, the outer sporogenous cell developed the embryo sac. At the same time, the epidermal cells at the tip of the nucellus divide periclinally. No evidence was found to indicate that a primary parietal cell is ever cut off by the archesporium.

EMBRYO SAC.—As the ovule develops, the funiculus increases greatly in length, and this is accompanied by a corresponding lengthening of the outer integument (*fig. 2*). At the same time the integuments thicken considerably, and leave a narrow space between the nucellus and the inner integument. The embryo sac lengthens downward and encroaches somewhat on the chalaza (*fig. 3*). Preparations of sacs were obtained containing two, four, and eight nuclei. In the preparation represented in *fig. 3* (three sections of a single sac) there were eight active nuclei, but also traces of several degenerate nuclei, apparently indicating that more than eight nuclei had been formed. In *fig. 3a* there appears to the left a small nucleus with feebly defined boundary, but abundant chromatin contents; two similar but smaller nuclear fragments appear in *fig. 3b*. All this perhaps indicates the presence of ten or twelve nuclei in the embryo sac, some of which break down.

Three of the eight active nuclei form the egg-apparatus (*fig. 4*). Fusion of the polar nuclei was not demonstrated, nor were any of the phases of fertilization well shown except in one case (*fig. 12*).

The number of antipodals is variable; for example, there are three in *fig. 5*, two in *fig. 6*, and four in *fig. 11*.

ENDOSPERM.—The endosperm begins with free nuclear division. Whether it originates from a single endosperm nucleus, or by direct divisions of six of the eight nuclei previously figured could not be satisfactorily determined. In *fig. 5* walls are beginning to appear between the free nuclei and it seems that the wall-formation begins at the middle of the sac and proceeds toward the ends.

The walls of the endosperm cells soon become heavy (*figs. 6, 7, 8*). When the embryo reaches the stage shown in *fig. 8*, the thickening of the endosperm walls is complete, and the nuclei begin to show a tendency to disintegrate.

EMBRYO.—The first divisions of the fertilized egg were not found. The earliest stage observed is shown in *figs. 6* and *8*, showing a spherical proembryo without a suspensor. The proembryo is usually at the upper extremity of the sac, but its position is extremely variable. *Fig. 9* represents a somewhat older embryo, a slight notch beginning to show on one side, which at later stages becomes more pronounced (*fig. 10*). At the same time the endosperm is gradually destroyed, and the embryo finally assumes the form shown in *fig. 11*, the endosperm having disappeared completely.

POLYEMBRYONY.—The sections shown in *figs. 6, 7*, and *8* were cut from the same sac. *Fig. 6* shows the embryo developed from the fertilized egg, and also a synergid; while in *fig. 8* another embryo is shown. These two sections cannot be different sections of the same embryo, for there are several intervening sections which show endosperm only, one of which is represented in *fig. 7*. It should be noted also that the second embryo (*fig. 8*) is not lower down in the sac than the one shown in *fig. 6;* in fact, the two lie side by side. All of the sac lying above the embryo in *fig. 8* represents a lateral upward extension of the sac not shown in *fig. 6*. This would suggest that the second embryo may have been derived from a synergid.

2. DIEFFENBACHIA DARAQUINIANA

In the material collected in the greenhouses of the New York Botanical Gardens, some was obtained from specimens labeled *Dieffenbachia daraquiniana*. This specific name is recognized neither by SCHOTT nor ENDER, and the species is probably identical with the one listed by the latter as *D. baraquini*.[1] The genus is notable in that the spadix is adherent along one side to the broad spathe, in which it is more or less tightly inclosed, the flowers occurring on the opposite side of the spadix. In the species under discussion the flowers were found scattered irregularly over the free surface of the spadix, crowded in places, but usually standing far apart and showing between them bits of the surface of the spadix. The male flowers occupy the upper part of the spadix, the female flowers the lower, the latter consisting only of an ovary. No traces of floral envelopes

[1] ENDER, Index Aroidearum 43. Berlin. 1864.

are present, but many staminodia are inserted near the base of the ovaries.

Ovary.—In the youngest material examined, the beginning of the flower appears as a slight protuberance on the surface of the spadix. A transverse crease soon appears, dividing this into two ill-defined lobes (*fig. 13*) which are destined to develop into the two carpels, and between the carpels appears the placenta, representing the axis of the flower (*fig. 14*). The carpels rapidly increase in size and overtop the placenta (*figs. 15, 16*). At the same time the ovules appear as lateral outgrowths of the placenta, filling the two cavities formed by the growth of the carpels (*fig. 15*). The continued growth of the carpels causes them to approach each other until there is left between them only a narrow canal, which divides over the apex of the placenta in such a way that the two branches lead down into the cavities of the carpels (*fig. 17*). On the upper and inner surface of each carpel, and leading down to the stylar canal, occurs a circular patch of somewhat viscid stigmatic cells (*fig. 17*).

Ovule.—The ovule first appears as a dome-shaped mass of undifferentiated cells projecting laterally into the carpellary cavity (*fig. 15*). The inner integument soon appears as an ill-defined ring about the upper portion of the ovule, and by the time the carpel has partially covered the placenta, the integument has grown out even with the apex of the nucellus, and the outer integument has begun to appear (*fig. 16*). At this stage the ovule is orthotropous. The lower surface now ceases to develop, while the upper continues to grow, thus finally making the ovule anatropous. At the same time, the integuments lengthen greatly, the outer one much exceeding the inner one (*fig. 17*).

Archesporium.—Before the ovule becomes anatropous, the archesporial cell may be recognized by its greater size and by its nucleus (*fig. 19*). Before the first division of the archesporium the overlying epidermal cells usually divide once (*fig. 20*). The archesporial cell, which in this case is the mother cell, gives rise to four megaspores (*fig. 21*), the outermost one of which produces the embryo sac.

Embryo sac.—The functioning megaspore increases greatly in size, destroying as usual the other megaspores and some of the adjacent tissue. When the outer integument has closed over the nucellus, the first nuclear division in the embryo sac usually occurs (*fig. 22*). This is followed by the usual divisions (*figs. 23, 24, 25*), until eight nuclei are formed, which assume the usual positions. In this case the polar fusion was observed (*figs. 24, 25*). Before the embryo sac is complete, the lateral tissue of the nucellus has usually disappeared, only the tissue at the tip remaining.

FERTILIZATION.—Although the material was at the proper stage to show fertilization, good preparations were very difficult to obtain. The best are shown in *figs. 26, 27, 28*, and double fertilization is evident.

ENDOSPERM.—Before the first division of the fertilized egg takes place, the embryo sac has increased greatly in size and has become almost completely filled with endosperm. The endosperm begins with free nuclear division, which continues until numerous nuclei are distributed through the sac. Later wall-formation occurs (*fig. 28*) and the sac is filled with tissue.

EMBRYO.—At the close of the free nuclear stage of the endosperm the fertilized egg divides transversely (*figs. 29, 30*); then longitudinal and transverse divisions follow in no definite sequence until the spherical proembryo is produced (*fig. 28*).

CHROMOSOMES.—The preparations of Dieffenbachia were unusually favorable for a definite count of chromosomes, and the alternating numbers were found to be eight and sixteen.

3. AGLAONEMA VERSICOLOR

Flowering material of this East Indian species was also obtained from the New York Botanical Gardens. The earlier stages of the microsporangium were not found, but quite a complete series was obtained showing the development of the megasporangium.

MICROSPORANGIUM.—In the youngest material examined the tapetum and middle wall layers had disappeared, leaving only the distinct endothecium overlaid by the epidermis. At this stage the mother cells have rounded off and are forming the tetrads. In older material the division into tube and generative nuclei was observed and eight chromosomes were counted (the reduced number).

MEGASPORANGIUM.—Aglaonema has one carpel containing a single anatropous ovule, which is cauline, although its lateral position at maturity might suggest that it is carpellary in origin (*fig. 33*). The stigmatic surface is prominent, and the cavity of the stylar canal is partially filled by a mass of similar cells, and long conducting cells extend downward on either side of the ovule, reaching the vicinity of the micropyle. At an early period the inner integument closes over the tip of the nucellus, but the outer integument does not close over the inner (*fig. 33*).

The earliest satisfactory preparations of the embryo sac show the first division (*fig. 36*) and the second (*fig. 37*). The final stages show great irregularity. *Fig. 38* shows a group of three cells (to the right) which suggests the egg apparatus; the two cells at the extreme left are certainly antipodals; while the two in the middle are evidently fusing polar nuclei. The solitary cell to the left suggests the third antipodal, but a male cell appears to be fusing with it. The ninth cell may be the other male nucleus. The embryo sac represented in *fig. 39* contains only five cells, two of which are clearly fusing polar nuclei.

The number of antipodals varies from two to eleven, and it is quite possible that they may sometimes be even more numerous (*figs. 33, 34, 35, 40*).

ENDOSPERM.—In Aglaonema the endosperm does not begin with free nuclear division, as in Dieffenbachia, Nephthytis, and Arisaema, but wall-formation begins at once. The growing endosperm first lines the side of the embryo sac which is toward the funiculus, but later fills the cavity and completely surrounds the embryo (*figs. 33, 40, 41, 42*).

EMBRYO.—The embryo much resembles that of *Lysichiton kamschatcense* as figured by CAMPBELL.[2] *Fig. 41* represents the position in which the proembryo was most frequently found, but in many cases it appears at the micropylar extremity of the sac. It appears quite as frequently adhering to the surface opposite the growing endosperm, and in at least one case was found resting on the antipodals. There was no evidence of displacement by sectioning, so that this variable position is probably due to the fact that the egg may lie in any part of the embryo sac.

BLAIRSTOWN, N. J.

[2] CAMPBELL, D. H., Notes on the structure of the embryo sac in Sparganium and Lysichiton. BOT. GAZETTE 27:153–166. 1899.

EXPLANATION OF PLATES IV–VI

PLATE IV

Nephthytis Gravenreuthii

FIG. 1.—Section of tip of ovule, showing massive integuments, small nucellus, and two sporogenous cells.

FIG. 2.—Ovary at somewhat later stage.

FIG. 3.—Three adjoining sections of the same embryo sac, showing eight vigorous nuclei and traces of two or three others.

FIG. 4.—Egg-apparatus.

FIG. 5.—Antipodals, and endosperm nuclei with incipient wall-formation.

FIG. 6.—Endosperm at a later stage, proembryo (*e*), and a persistent synergid (*s*).

FIG. 7.—Endosperm.

FIG. 8.—Second proembryo in same sac shown in *fig. 6*.

FIG. 9.—Proembryo.

FIG. 10.—Embryo showing notch.

FIG. 11.—Mature embryo.

FIG. 12.—Fertilization, showing pollen tube (*p*), egg (*o*), male cell (*m*), and synergid (*s*).

PLATE V

Dieffenbachia daraquiniana

FIG. 13.—First appearance of carpels.

FIG. 14.—Later stage.

FIG. 15.—First appearance of ovule.

FIG. 16.—Later stage, showing nucellus (*n*) and integuments (*i, o*).

FIG. 17.—Section of ovary, showing stigmatic surface (*st*), stylar canal (*s*), and the anatropous ovules.

FIG. 18.—Section of ovule showing an embryo sac containing endosperm nuclei (*e*); the other structures are evident.

FIG. 19.—The archesporial cell.

FIG. 20.—Division of epidermal cells.

FIG. 21.—The linear tetrad, the outermost megaspore (*m*) functional.

FIGS. 22–25.—Stages in the development of the sac.

FIG. 26.—Fertilization of egg.

FIG. 27.—Fusion of male cell with endosperm nucleus.

FIG. 28.—Free endosperm nuclei.

FIG. 29.—Endosperm at later stage, and proembryo.

FIGS. 30–32.—Early divisions in proembryo-formation.

PLATE VI

Aglaonema versicolor

FIG. 33.—Ovary with the solitary ovule; embryo sac containing embryo (*e*), endosperm (*n*), and antipodals (*a*).

FIG. 34.—Group of eleven antipodals.

FIG. 35.—Group of three antipodals.

FIG. 36.—First nuclear division in embryo sac.

FIG. 37.—Four-nucleate sac.

FIG. 38.—Eight-nucleate sac and two male cells (one fusing with a cell).

FIG. 39.—Fusion of polar nuclei.

FIG. 40.—Older sac, showing endosperm (*n*) and antipodals (*a*).

FIG. 41.—Sac showing endosperm (*s*) and proembryo (*e*).

FIG. 42.—Diagram showing later development of embryo (*n*) and endosperm (*e*).